Conservation Biology

Research Note

Predicting Interactions among Fishing, Ocean Warming, and Ocean Acidification in a Marine System with Whole-Ecosystem Models

GARY P. GRIFFITH,*†§ ELIZABETH A. FULTON,‡ REBECCA GORTON,‡ AND ANTHONY J. RICHARDSON†

*Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, Private Bag 129, Hobart, Tasmania 7001, Australia
†Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, Ecosciences Precinct, GPO Box 2583, Brisbane, Qld 4001, Australia
‡Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, Tasmania 7001, Australia

Abstract: *An important challenge for conservation is a quantitative understanding of how multiple human stressors will interact to mitigate or exacerbate global environmental change at a community or ecosystem level. We explored the interaction effects of fishing, ocean warming, and ocean acidification over time on 60 functional groups of species in the southeastern Australian marine ecosystem. We tracked changes in relative biomass within a coupled dynamic whole-ecosystem modeling framework that included the biophysical system, human effects, socioeconomics, and management evaluation. We estimated the individual, additive, and interactive effects on the ecosystem and for five community groups (top predators, fishes, benthic invertebrates, plankton, and primary producers). We calculated the size and direction of interaction effects with an additive null model and interpreted results as synergistic (amplified stress), additive (no additional stress), or antagonistic (reduced stress). Individually, only ocean acidification had a negative effect on total biomass. Fishing and ocean warming and ocean warming with ocean acidification had an additive effect on biomass. Adding fishing to ocean warming and ocean acidification significantly changed the direction and magnitude of the interaction effect to a synergistic response on biomass. The interaction effect depended on the response level examined (ecosystem vs. community). For communities, the size, direction, and type of interaction effect varied depending on the combination of stressors. Top predator and fish biomass had a synergistic response to the interaction of all three stressors, whereas biomass of benthic invertebrates responded antagonistically. With our approach, we were able to identify the regional effects of fishing on the size and direction of the interacting effects of ocean warming and ocean acidification.*

Keywords: climate change, ecosystem management, fisheries, predictive modeling

Predicción de Interacciones entre Pesca, Calentamiento de Océanos y Acidificación de Océanos en un Sistema Marino con Modelos de Ecosistemas Completos

Resumen: *Un reto importante para la conservación es el entendimiento cuantitativo de la forma en que interactúan múltiples factores estresantes humanos para mitigar o exacerbar el cambio climático global a nivel de comunidad o ecosistema. Exploramos los efectos temporales de la interacción de la pesca, el calentamiento de océanos y la acidificación de océanos sobre 60 grupos funcionales de especies en el ecosistema marino del sureste de Australia. Monitoreamos cambios en la biomasa relativa en el marco de un modelo dinámico acoplado de ecosistema completo que incluyó el sistema biofísico, efectos humanos, socioeconómicos y evaluación del manejo. Estimamos los efectos individuales, aditivos e interactivos sobre el ecosistema y sobre*

§*email gary.griffith@utas.edu.au*
Paper submitted November 06, 2011; revised manuscript accepted June 07, 2012.

Conservation Biology, Volume 00, No. 0, 1–8

DOI: 10.1111/j.1523-1739.2012.01937.x

5 grupos de la comunidad (depredadores superiores, peces, invertebrados bentónicos, plancton y productores primarios). Calculamos el tamaño y dirección de los efectos de la interacción con un modelo aditivo nulo e interpretamos los resultados como sinérgicos (estrés amplificado), aditivos (sin estrés adicional) o antagónicos (estrés reducido). Individualmente, solo la acidificación de océanos tuvo un efecto negativo sobre la biomasa total. La pesca y el calentamiento de océanos y el calentamiento de océanos con acidificación de océanos tuvieron un efecto aditivo sobre la biomasa. Al añadir la pesca al calentamiento de océanos y la acidificación de océanos, hubo cambio significativo en la dirección y magnitud del efecto de interacción a una respuesta sinérgica sobre la biomasa. El efecto de interacción dependió del nivel de respuesta examinado (ecosistema vs. comunidad). Para comunidades, el tamaño, dirección y tipo de efecto de interacción variaron dependiendo de la combinación de estresantes. Los depredadores superiores y la biomasa de peces tuvieron una respuesta sinérgica a la interacción de los 3 estresantes, mientras la biomasa de los invertebrados bentónicos respondió antagonistamente. Mediante nuestro método, pudimos identificar los efectos regionales de la pesca sobre el tamaño y dirección de los efectos interactivos del calentamiento y acidificación de los océanos.

Palabras Clave: Cambio climático, manejo de ecosistemas, modelo predictivo, pesquerías

Introduction

Multiple human stressors affect many terrestrial and marine systems (Halpern et al. 2008) and interact in complex and often unpredictable ways. For instance, in the North Sea, ocean warming has led to a shift of the planktonic ecosystem toward dominance by smaller organisms and thus to increased biodiversity. However, the interaction among ocean warming, decline in planktonic species, increase in smaller demersal species, and change in fishing practices has led to reduced stability and resilience of the ecosystem (Beaugrand et al. 2010).

The effect of multiple stressors is often assumed to be the additive effect of the individual stressors (Halpern et al. 2007). The combined effect of multiple stressors can either be the simple addition of the effects of individual stressors or greater than (synergistic) or less than (antagonistic) of the sum of individual effects (Folt et al. 1999). In management, additive interactions have a predictable effect. Reducing the magnitude of any stressor should lead to a corresponding increase in the response of interest that should be predictable from studies on the effects of a single stressor. A synergistic effect is generally considered to have harmful consequences for ecological systems and to amplify negative effects potentially pushing ecosystems into alternative states. Antagonistic interactions should mitigate the effect and be less damaging to biodiversity. There is a prevailing view that stressors act synergistically. The few studies that have explicitly evaluated the nature of interactions between stressors show that all interaction types commonly occur when two stressors interact; this result suggests that synergies may be less common than predicted (Crain et al. 2008; Darling & Côté 2008). In the more realistic situation of three or more stressors, synergies are expected to be the most prevalent interaction type (Paine et al. 1998).

With the increasing concern that multiple human effects will interact synergistically to accelerate biodiversity loss, there is a need to quantitatively understand how these effects scale up to communities and ecosystems. Here we examined how whole-ecosystem and community responses to multiple stressors can be understood on the basis of interaction type, and the magnitude and direction of the interaction effect. We investigated the individual and interactive effects of fisheries, ocean warming, and ocean acidification to the year 2050 on the southeastern Australian marine ecosystem. We addressed the effect of each stressor, the interactive effect of combinations of the stressors, and whether the interaction effect changed at the community and ecosystem level.

Methods

Study Area

The study area encompassed the southeastern Australian marine ecosystem. This region covers 3.7 million km^2 of Australia's exclusive economic zone (24°21′S, 160°30′E to 46°51′S, 117°48′E). The area includes tropical, subtropical, cool temperate, and subantarctic environments (Bulman et al. 2006). The region has been commercially fished for 150 years and currently produces over 50% of the gross value of Australia's fisheries (Fulton et al. 2007). Over 148 species are harvested commercially, ranging from invertebrates such as the southern rock lobster (*Jasus edwardsii*) to long-lived, deepwater fish species such as orange roughy (*Hoplostethus atlanticus*). A regional marine plan that aims to protect, conserve, and restore the region's marine biodiversity and ecological processes has been implemented (National Oceans Office 2004).

Model Description

Over the past 10 years, a largely deterministic whole-of-ecosystem model known as Atlantis-SE has been developed for the region (Fig. 1) (full documentation is available from http://atlantis.cmar.csiro.au/). Atlantis-SE is a modeling framework intended for evaluation of regional

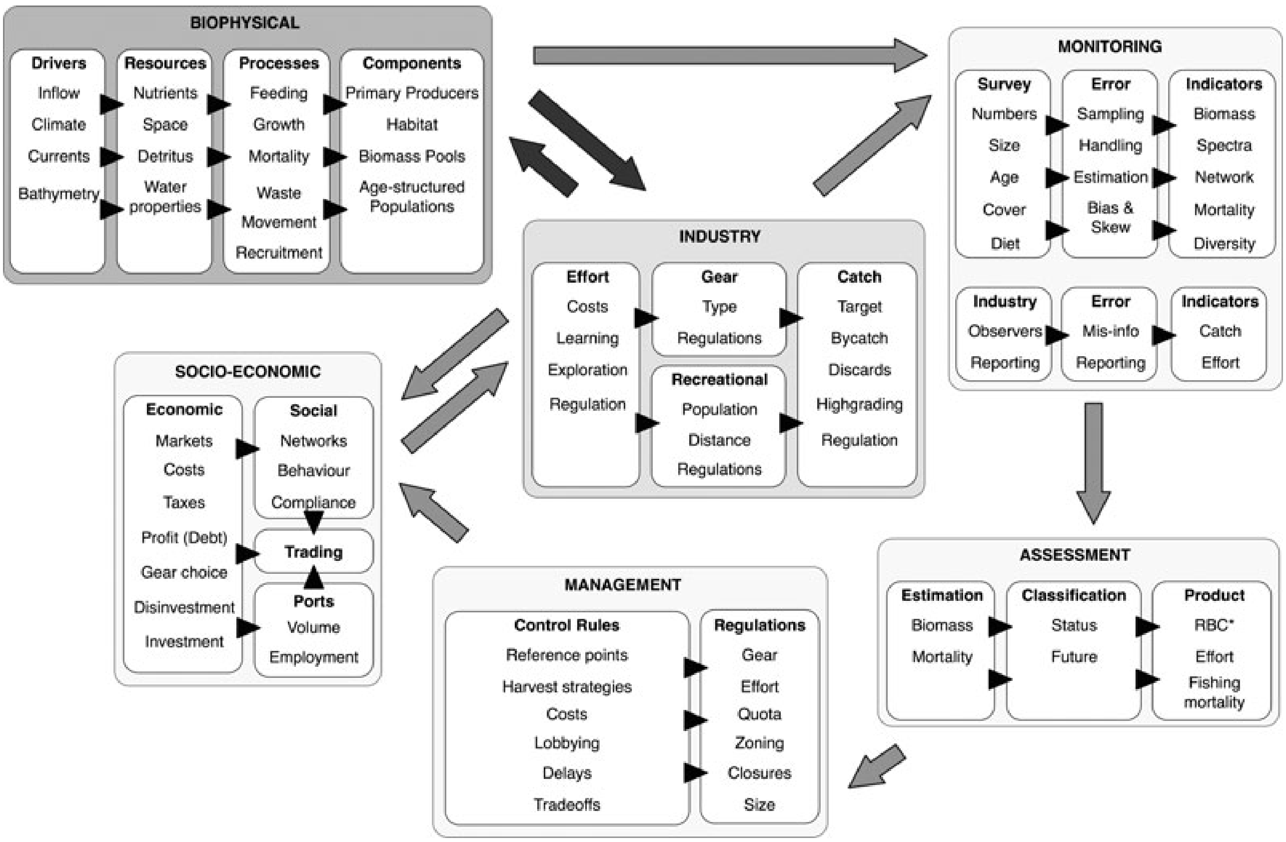

Figure 1. Components, connections, and major processes included in the Atlantis-SE modeling framework (RBC, recommended biological catch).

management strategies (Fulton et al. 2011). The model was built on a largely deterministic, spatially resolved, three-dimensional, biophysical submodel that tracks nutrient flow through the main biological groups on 6- to 24-hour time steps. Sixty functional groups are represented including age-structured fish stocks, some resolved to species (Supporting Information). The groups are defined on the basis of a range of options, including consumption, production, movement, recruitment, and habitat dependency. Model output from the biotic components includes changes in biomass, mortality, and predator–prey interactions.

The physical environment is spatially resolved in three dimensions (up to five depth layers) and the geographic region is represented by irregular polygons matched to the major geomorphological and bioregional features. The model has a detailed exploitation submodel that interacts with the biotic parts of the model and includes anthropogenic effects such as pollution, coastal development, fishing, and climate effects. Output from these submodels is applied in a management submodel that addresses the biological, social, and economic consequences of different model scenarios. Atlantis-SE has been extensively calibrated with fish-catch data and other data from commercial fisheries and data from scientific surveys conducted within the region over the past 90 years. The model has been used to evaluate general fisheries issues, such as multispecies maximum sustainable yield (Worm et al. 2009), to explore questions concerning the usefulness of ecological indicators for fisheries (Branch et al. 2010), and climate change (Griffith et al. 2011).

Within the model, fishing is represented by the current quota-management system for 13 types of fisheries: purse-seine, demersal-line, pelagic-line, dredge, dive, jig, demersal (bottom trawl), midwater-trawl, trap, gill-net, Danish seine, and recreational fisheries. The fisheries management regulations and decisions to year 2050 were based on those current at year 2011 for southeastern Australia. The amount and type of fish harvested varied dynamically depending on year-to-year quotas and stock status.

Ocean warming was simulated on the basis of oceanographic output from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Mk 3.5 climate system model (Gordon et al. 2010) derived from the Intergovernmental Panel on Climate Change (IPCC) Special Report Emissions Scenerio (SRES) A2 scenario (IPCC 2007). Ocean warming trends were incorporated into the existing oceanographic submodel within the Atlantis-SE model to create a reconstructed regional temperature and salinity time series from 2000 through

2050. The reconstructed time series was validated from field measurements taken off the southeastern Australian coast from 2000 through 2010.

For southeastern Australia, the IPCC IS92a scenario, "business-as-usual" CO_2 emission, predicted a pH change from the current approximately 8.1 to approximately 7.8 by 2100. We used the business-as-usual scenario to calculate a change in ocean chemistry for the region from a pH of 8.07 in 2000 to a pH of 7.92 by 2050. Although there is little understanding of the effects of ocean acidification on many species (Blackford 2010), in situ observations and laboratory studies show that ocean acidification increases mortality of benthic-shelled organisms (Kurihara et al. 2007; Kurihara et al. 2009). Using empirical observations and the predicted change in oceanic pH for the region, we modelled an additional mortality on the benthic invertebrate groups of between 0.1% per day and 0.3% per day (Griffith et al. 2011).

Interaction Effects

We calculated the individual, additive, and interaction effect sizes for each model scenario with Hedge's d, which is similar to analysis of variance in that a significant interaction effect indicates deviation from the null model of additivity (Hedges & Olkin 1985; Morris et al. 2007; Crain et al. 2008). Individual effects represented the response to one stressor versus the control, whereas the additive effects related the net response to a stressor in the presence of a second or third stressor. Here, the response variable was the change in relative biomass of each functional group or species in response to each stressor or stressor combination from 2010 through 2050. The interaction effect size was calculated for the following stressor combinations: fishing and ocean warming; fishing and ocean acidification; ocean warming and ocean acidification; and all three stressors (Supporting Information). The control was no fishing, no ocean acidification, and no ocean warming. With a conceptual model (Crain et al. 2008), we used the interaction effect size and 95% CI to classify the effect of stressor combinations as antagonistic (reduced stress), additive (no additional stress), or synergistic (amplified stress). For stressor combinations whose individual or additive effects were either all negative or had 1 or 2 negative and 1 positive value, interaction effect sizes whose 95% CI overlapped zero were classified as additive. Interaction effect sizes of <0 were considered synergistic, and interaction effect sizes >0 were antagonistic. When individual or additive effects were all positive, interactions were interpreted in the opposite manner (Supporting Information).

Community-level variables appear to be more sensitive to stressors than ecosystem-level variables and may be more useful for detecting interaction effects (Fulton et al. 2011). To investigate the contribution of each of the stressors to the community-level response to multiple stressors, we aggregated the 54 functional groups and species into five community groups (top predators, fishes, benthic invertebrates, plankton, and primary producers).

Results

Ocean acidification had a significant negative effect on biomass, whereas neither fishing nor ocean warming had a significant effect on changes in biomass. Fishing and ocean warming together had an additive effect on biomass. Ocean warming and ocean acidification together also had an additive effect on biomass (Fig. 2b). Fishing and ocean acidification and fishing, ocean acidification, and ocean warming had a synergistic effect on changes in biomass. Types of interactions varied among community groups and stressor combinations (Fig. 3a–e). The response to all three stressors was greater among the higher trophic organisms (top predators and fishes). Ocean warming and ocean acidification had an antagonistic effect on primary producers; the addition of fishing reduced the antagonistic response. The addition of fishing as the third stressor reduced the percentage of species that responded antagonistically to ocean warming and ocean acidification (from 65% to 25%) and doubled the percentage of synergistic interactions (from 25% to 53%) (Fig. 4).

Discussion

For the southeastern Australian marine ecosystem, the combination of fishing with ocean warming and of ocean warming with ocean acidification was additive and could be predicted from the simple addition of the effects of the individual stressors. By contrast, the combination of fishing and ocean acidification was synergistic. The most realistic scenario of the interaction all three stressors resulted in an overall synergistic response of biomass. This is consistent with the view that multiple stressors generally interact synergistically in marine systems (Crain et al. 2008).

At the community level, a range of interaction effect sizes occurred, and interaction types suggest synergisms should not be assumed. The community response to multiple stressors helped us predict and interpret the interaction effects. For instance, as expected, fishing had the largest negative effect on the synergistic response by fish to the interaction of the three stressors. However, our approach also showed an increasing negative effect of ocean warming over time, a result that is consistent with the view that growth rates in temperate fish species will initially increase as ocean temperatures rise but decline as metabolic demands increase (Neuheimer et al. 2011).

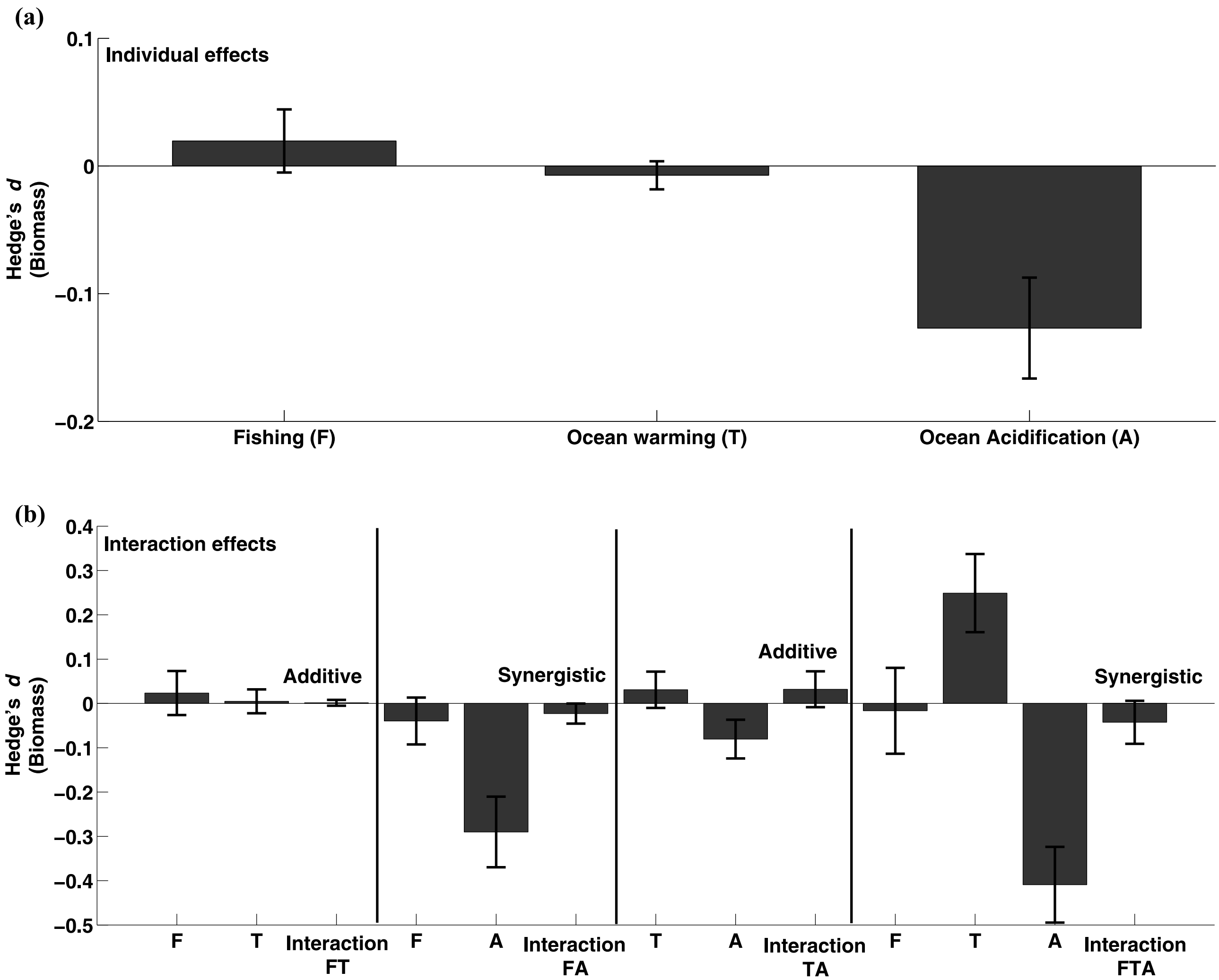

Figure 2. Individual, additive, and interaction effect sizes; interaction type (Hedge's d); and 95% CI for the entire Australian southeastern ecosystem (n = 60): (a) individual stressor effects for fishing, ocean warming, and ocean acidification and (b) additive effect and interaction type for the overall ecosystem.

The interactions of the three stressors resulted in some responses that were unexpected. The benthic invertebrate group responded antagonistically to the interaction effects, although we used increased mortality on species within this group as a proxy for acidification effects. Fishing decreased predator pressure on the benthic invertebrate group and overcompensated for the negative effects of acidification. Top predators, plankton, and primary producers responded synergistically to ocean acidification, the main contributor to the decrease in biomass of these groups.

At the ecosystem level, the interaction effects of the stressor combinations helped us identify the role regional fishing may play in determining the size and direction of interaction effects from climate change, such as ocean warming and ocean acidification. Reduced fishing may mitigate effects of ocean warming and ocean acidification. Response variables may respond to the removal or reduction of a single stressor as long as the ecosystem can revert to a previous state (Gurevich et al. 2000). Reduction of ocean warming and ocean acidification will require a global response, whereas the effects of fishing can be mitigated relatively quickly through regional management action (Cooley & Doney 2009).

Our findings show that the variation in interaction response at the community level must also be considered. A reduction in fishing could reduce the expected synergistic response of the three stressors on the community biomass of the fish group and reduce the antagonistic response to benthic invertebrates. Ocean acidification, not fishing, was the principle driver in the interaction effect of the three stressors on top predators, plankton, and primary producers. Our approach provides a mechanism that can be used to understand and interpret complex interaction effects and how these effects scale up to communities and ecosystems.

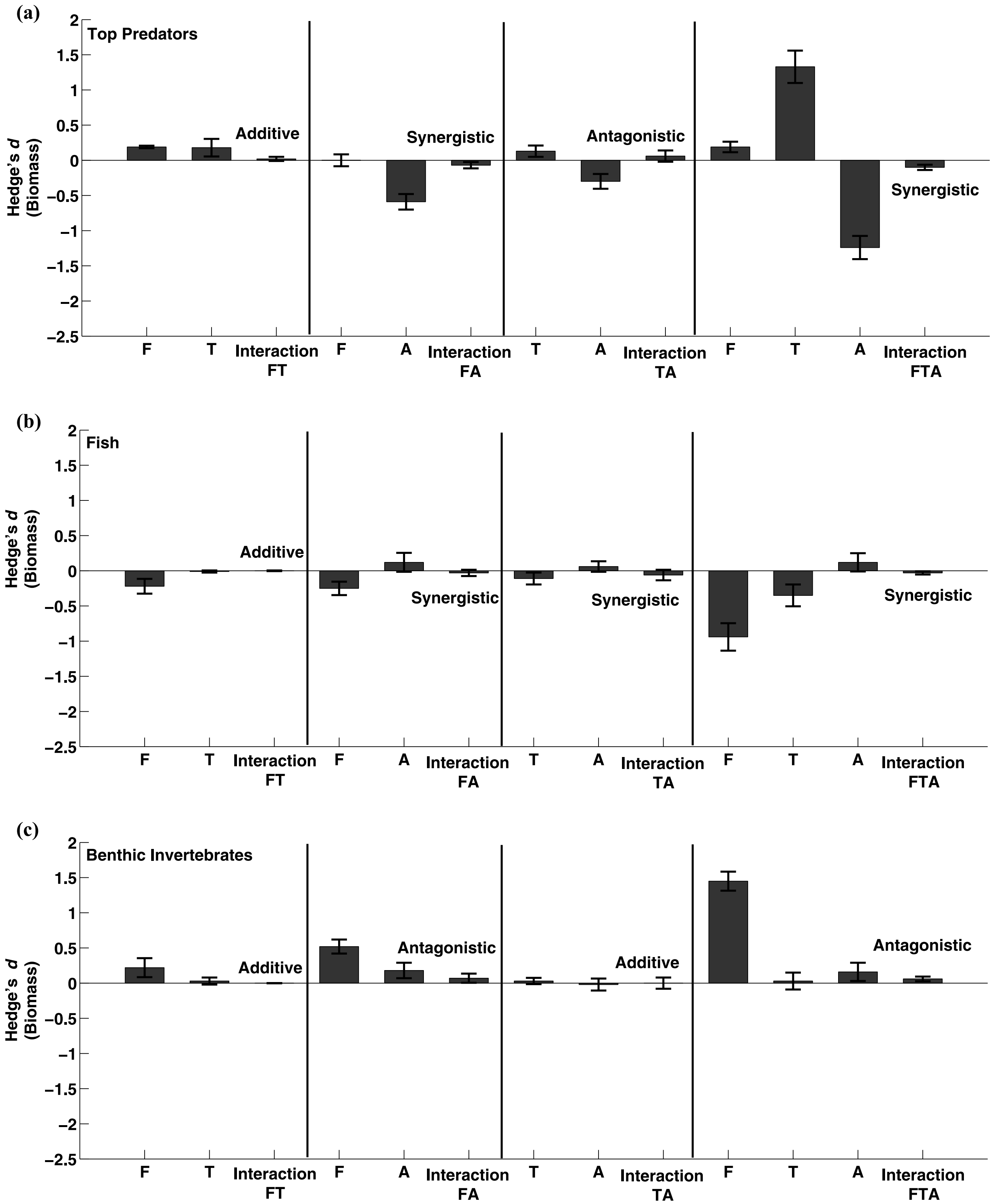

Figure 3. Additive effects, interaction effects, interaction type (Hedge's d), and 95% CI for the community groups: (a) top predators (n = 12), (b) fish (n = 24), (c) benthic invertebrates (n = 9), (d) plankton (n = 4), and (e) primary producers (n = 5) (F, fishing; T, ocean warming; A, ocean acidification).

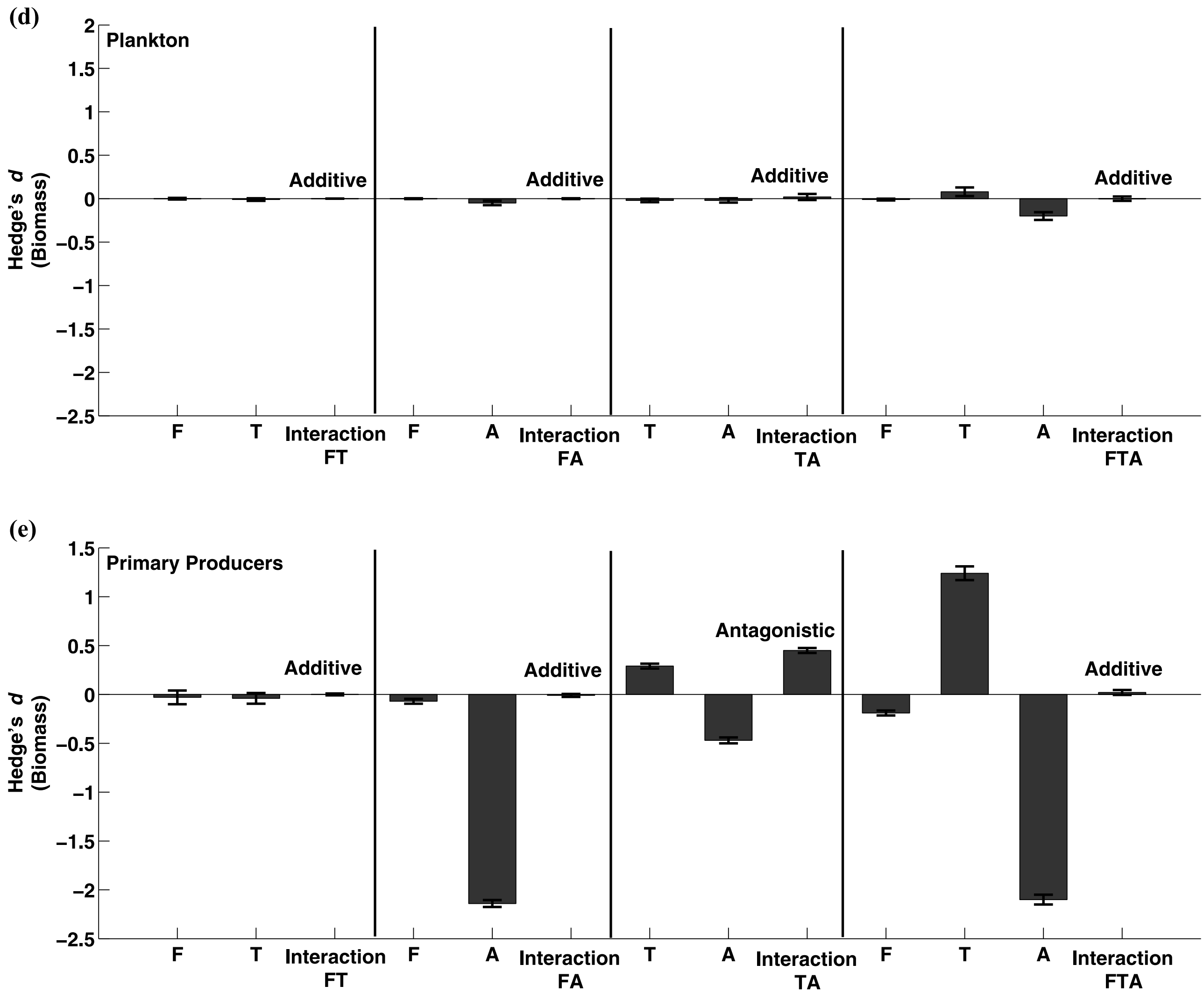

Figure 3. Continued.

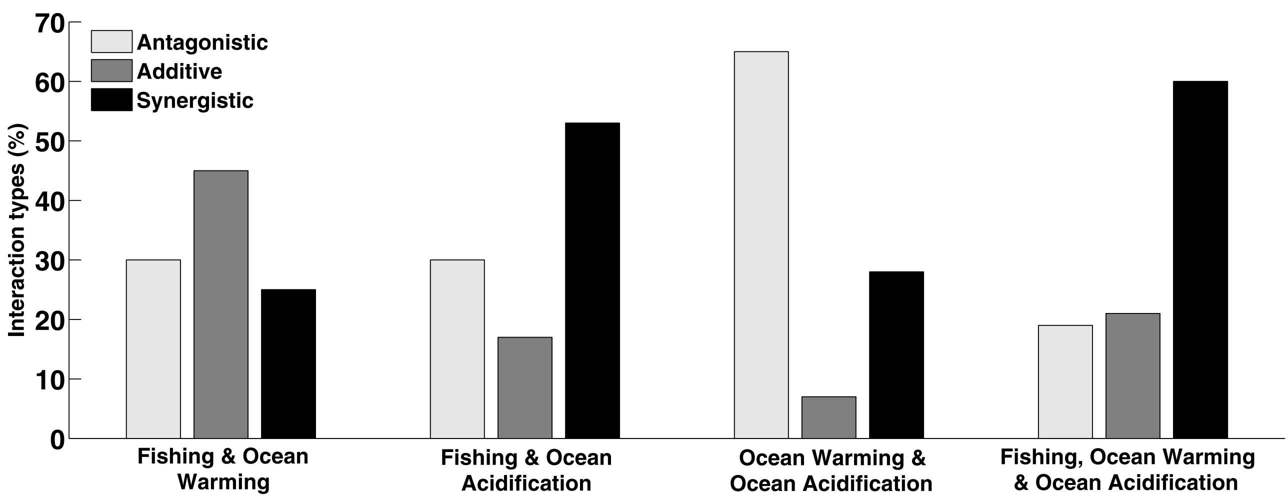

Figure 4. The frequency distribution of interaction types (antagonistic, additive, and synergistic) across the stressor combinations for species and functional groups (n = 60).

Acknowledgments

We thank W. Venables (CSIRO) for advice and assistance on statistical methods and three anonymous referees for helpful comments. The CSIRO Climate Adaptation Flagship Program and an Australian Research Council Discovery Grant supported this research.

Supporting Information

Equations for interaction effects, tables of interaction results, list of species and Atlantis-SE model equations (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

Literature Cited

Beaugrand, G., M. Edwards, and L. Legendre. 2010. Marine biodiversity, ecosystem functioning and carbon cycles. Proceedings of the National Academy of Sciences of the United States of America **107:**10120–10124.

Blackford, J. C. 2010. Predicting the impacts of ocean acidification: challenges from an ecosystem perspective. Journal of Marine Systems **81:**1–18.

Branch, T. A., et al. 2010. The trophic fingerprint of marine fisheries. Nature **468:**431–435.

Bulman, C., et al. 2006. Trophic dynamics of the eastern shelf and slope of the southeast fishery: impacts of and on the fishery. Final report project 2002/028 CSIRO. Commonwealth Scientific and Industrial Research Organisation, Hobart, Tasmania.

Cooley, S. R., and S. C. Doney. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. Environmental Research Letters **4:**024007.

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters **11:**1304–1315.

Darling, E. S., and I. M. Côté. 2008. Quantifying the evidence for ecological synergies. Ecology Letters **11:**1278–1286.

Folt, C. L., C. Y. Chen, M. V. Moore, and J. Burnaford. 1999. Synergism and antagonism among multiple stressors. Limnology and Oceanography **44:**864–877.

Fulton, E. A., A. D. M. Smith, and D. C. Smith. 2007. Alternative management strategies for southeast Australian Commonwealth Fisheries: stage 2: quantitative management strategy evaluation. Australian Fisheries Management Authority, Fisheries Research and Development Corporation, Canberra.

Fulton, E. A., et al. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries **12:**171–188.

Gordon, H., et al. 2010. The CSIRO Mk 3.5 climate model. Technical Report 021. Centre Australian Weather and Climate Research (CAWR), Melbourne, Australia.

Griffith, G. P., E. A. Fulton, and A. J. Richardson. 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. Global Change Biology **17:**3058–3074.

Gurevich, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. The American Naturalist **155:**435–453.

Halpern, B. S., K. Selkoa, F. Micheli, and C. Kappel. 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conservation Biology **21:**1301–1315.

Halpern, B. S., K. L. Mcleod, A. A. Rosenberg, and L. B. Crowder. 2008. Managing for cumulative impacts in ecosystem based management through ocean zoning. Ocean Coastal Management **51:**203–211.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, New York.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth assessment report of the Intergovernmental Panel on Climate Change. United Nations Environmental Programme and the World Meteorological Organisation, Geneva. Available from http://www.ipcc.ch/publications_and_data/ar4/wg2/en/contents.html (accessed August 2012).

Kurihara, H., S. Kato, and A. Ishimatsu. 2007. Effect of increased seawater pCO_2 on early development of the oyster *Crassostrea gigas*. Aquatic Biology **1:**91–98.

Kurihara, H., et al. 2009. Effect of increased seawater pCO_2 on early development of the mussel *Mytilus galloprovincialis*. Aquatic Biology **4:**225–223.

Morris, W. F., et al. 2007. Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. Ecology **88:**1021–1029.

National Oceans Office. 2004. South-east regional marine plan, implementing Australia's oceans policy in the South-east Marine Region. National Oceans Office, Canberra. Available from http://www.environment.gov.au/coasts/mbp/publications/south-east/pubs/sermp.pdf (accessed August 2012).

Neuheimer, A. B., R. E. Thesher, J. M. Lyle, and J. M. Semmens. 2011. Tolerance limit for fish growth exceeded by warming waters. Nature Climate Change DOI:10.1038/NCLIMATE1084.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1:**535–545.

Worm, B., et al. 2009. Rebuilding global fisheries. Science **325:**578–585.